

**Dissertationes Forestales 305**

**Vegetation, nutrients, and CO<sub>2</sub> flux dynamics in northern  
boreal forests**

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*Academic dissertation*

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public examination in Auditorium B2, Forest Sciences Building (Viikki Campus, Latokartanonkaari 7, Helsinki) on December 16<sup>th</sup> 2020, at 13 o'clock.

*Title of dissertation:* Vegetation, nutrients, and CO<sub>2</sub> flux dynamics in northern boreal forests

*Author:* Laura Matkala

*Dissertationes forestales* 305

<https://doi.org/10.14214/df.305>

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ISSN 1795-7389 (online)

ISBN 978-951-651-700-4 (pdf)

ISSN 2323-9220 (print)

ISBN 978-951-651-701-1 (paperback)

*Printers:* Unigrafia, Helsinki 2020

*Cover photo:* Laura Matkala

*Publishers:*

Finnish Society of Forest Science

Faculty of Agriculture and Forestry at the University of Helsinki

School of Forest Sciences at the University of Eastern Finland

*Editorial Office:*

Finnish Society of Forest Science,

Viikinkaari 6, 00790 Helsinki, Finland

<http://www.dissertationesforestales.fi>

**Matkala L.** (2020). Vegetation, nutrients, and CO<sub>2</sub> flux dynamics in northern boreal forests. *Dissertationes Forestales* 305. 36 p. <https://doi.org/10.14214/df.305>

## ABSTRACT

The growing conditions in northern boreal forests have remained similar for millennia. However, amplified climate change may cause higher mean annual temperatures and precipitation sums, longer growing seasons, along with increased occurrence of extreme weather events (drought, heavy rain, or summertime frost) in the region. The relationship that forest vegetation has with soil nutrients and the exchange of carbon dioxide (CO<sub>2</sub>) between the forest and atmosphere may change. This dissertation focuses on quantifying the baseline status of northern boreal forests from these aspects, to be able to predict the upcoming changes more precisely. Soil total phosphorus (P) and nitrogen (N) contents were important factors in explaining the community composition of understory vegetation in the study site. The site was located in a region near a phosphate ore, where soil nutrient contents are highly variable. The number of herb, grass, and sedge species increased with N and P contents in the humus, especially with P. The increasing P content, on the other hand, positively correlated with downy birch (*Betula pubescens* Ehrh.), which was the dominant tree species of the research plot.

The understory vegetation had an important role in the CO<sub>2</sub> exchange rates of a northern boreal Scots pine (*Pinus sylvestris* L.) forest site. The annual CO<sub>2</sub> dynamics varied between the canopy and understory, so that when the canopy began photosynthesizing in the spring, the understory was still under snow cover. The cumulative temperature sum had a higher positive correlation with photosynthesis than the total ecosystem respiration (TER) rate of the pine site. Overall, the pine site was a weak carbon sink during the growing season, although it temporarily turned into a carbon source during a cold and rainy summer.

Extreme weather events, and their effects on the CO<sub>2</sub> dynamics of forests, were studied on a Scots pine site and a Norway spruce (*Picea abies* (L.) Karst.) site. Both sites had experienced extreme summers during the studied times, but the CO<sub>2</sub> flux rates in the Norway spruce site responded more clearly to them. The TER rates of the Norway spruce forest declined when it was warm and dry. This likely happened because of decreased decomposition of organic matter. The decline was, however, only temporary, and TER returned to normal when the temperature and precipitation returned to their average levels. Thus, the studied forest sites seemed to, so far, be rather resilient towards extreme weather events.

Several studies have found that N availability will increase because of warmer temperatures, which speeds up decomposition and nutrient mineralization. However, decomposition may potentially slow down in some spruce forests due to heat. Local variation may thus be high when it comes to the availability of nutrients or to the CO<sub>2</sub> dynamics of forests. While modeling studies are important for predicting the responses of northern forests to climate change on the large scale, our research reminds that local-scale studies are also inevitable for gaining a more precise picture.

**Keywords:** climate change, carbon, nitrogen, phosphorus, atmosphere, extreme events, northern boreal

## ACKNOWLEDGEMENTS

Never had I imagined that I would write the summary part of this dissertation in our kitchen during a time of social distancing caused by a pandemic. Yet, there I was, spending half the day intensively writing and half the day doing whatever it was that interested a three-year-old the most at that time. It is safe to say that the spring was a whirl of emotions from pure joy to frustration in all aspects of life.

Despite writing the summary in almost solitude, I would not have gotten this far without other people. I have been lucky to have two supervisors, who have encouraged and supported in good times, and when things have not gone as planned. I thank my main supervisor Prof. Jaana Bäck for trusting that I can do my work whether it is fieldwork in Lapland or writing in Helsinki. Every time I have had some issues with work, things have started to feel easier after talking to you. There was also a time when my motivation towards my own research was gone. You found me something else to do for a couple of months, and that was exactly what I needed. Dr. Liisa Kulmala has not been an official supervisor for very long, but has surely supervised my work for at least a couple of years when working on articles together. I admire your energy and positivity. You have the skills to give constructive feedback so that it does not let the other person down. I highly appreciate that as a young scientist who does not yet have much experience from writing scientific articles. My other co-authors have also been very helpful and patient. Special thanks to Dr. Maija Salemaa for persistently helping me with the first article and its analyses. Thank you senior lecturer Maj-Lena Linderson for accepting our invitation to act as my opponent. I also want to thank Prof. Eva-Stiina Tuittila and Assoc. prof. Matthias Peichl, who took time and carefully pre-examined this dissertation, and Stella Thompson, who corrected the grammar of the summary.

I am thankful for the Institute for Atmospheric and Earth System Research, Department of Forest Sciences and the Ecosystem processes research group for good working environment and facilities, and Academy of Finland ARKTIKO program and Maj and Tor Nessling Foundation for funding my work. Thank you lab magician Marjut Wallner for help with analyses and for fun company in the lab! I thank the permanent staff and the summer workers at Värriö Research Station for all the help, food and company (and sauna) during the two summers I stayed there. Dr. Sigrid Dengel was the person who first introduced me to Värriö and helped me in the beginning of my doctoral work, and I want to thank her for that.

Thank you, current and former office mates (Anna, Mari, Lauri, Kourosh, Anni, Kaisa) from room 321 for keeping the spirit high in the office. In addition to the gang in 321, I wish to thank current/former fellow doctoral students, especially Maiju, Lilli, Teemu, Niko, Elisa, Chari and Kira for peer support and fun times. If I forgot someone, forgive me. I have not seen most of you in a long time. Thank you also all the other friends for being a part of my life outside of work.

Isä, äiti ja muu perhe: iso kiitos tuesta ja siitä, että saatte minut unohtamaan työasiat niin tehokkaasti. Olli, thank you for peer support in science and in life, for everything! Also, thanks for helping with a bunch of unit conversions, which always caused me so much frustration (which you also bravely tolerated!). Finally, Kaarlo, äitin muru. Nothing makes me forget work like playing in puddles, or watching ants in the forest with you. Your enthusiasm and curiosity towards everything in life gives me joy and happiness every day.

Helsinki November 2020,  
Laura Matkala

## LIST OF ORIGINAL ARTICLES

This dissertation is based on the following four articles, which are referred to in the text by their Roman numerals. All papers are reproduced with the permission of the publisher.

- I. **Matkala, L.**, Salemaa, M., & Bäck, J. (2020). Soil total phosphorus and nitrogen explain vegetation community composition in a northern forest ecosystem near a phosphate massif. *Biogeosciences* 17(6): 1535-1556. <https://doi.org/10.5194/bg-17-1535-2020>
- II. Kulmala, L., Pumpanen, J., Kolari, P., Dengel, S., Berninger, F., Köster, K., **Matkala, L.**, Vanhatalo, A., Vesala, T., & Bäck, J. (2019). Inter- and intra-annual dynamics of photosynthesis differ between forest floor vegetation and tree canopy in a subarctic Scots pine stand. *Agricultural and Forest Meteorology* 271: 1-11. <https://doi.org/10.1016/j.agrformet.2019.02.029>
- III. **Matkala, L.**, Kulmala, L., Kolari, P., Aurela, M., & Bäck, J. (2020). Resilience of subarctic Scots pine and Norway spruce forests to extreme weather events. *Agricultural and Forest Meteorology* (in press) <https://doi.org/10.1016/j.agrformet.2020.108239>

## AUTHOR CONTRIBUTION

Laura Matkala (LM) was responsible for the summary of this thesis. In article **I**, LM was responsible for planning the study set up, conducted all fieldwork, laboratory and statistical analyses, and led the writing process. In article **II**, Liisa Kulmala was the corresponding author, LM was responsible for the practical planning of the biomass and growth increment measurements, and for conducting the measurements and analyzing the raw data, as well as served as a co-author of the article. In article **III**, LM was responsible for the data analyses, statistical analyses, and for leading the writing process.

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# 1. INTRODUCTION

## 1.1 Special features of northern boreal forests and potential future changes

The northern boreal subzone is located in the uppermost part of the boreal zone (Hämet-Ahti 1981). There, the subarctic climate shapes vegetation with cold temperatures and short growing seasons, which last approximately four months. The biological processes, such as growth or the decomposition of organic matter, and the following release of nutrients are slow (Hobbie et al. 2002). Unlike in the Arctic, where conditions do not allow tree regeneration, the northern boreal zone has forests. Typical northern boreal forests have lower precipitation rates than the more southern boreal subzones (Hämet-Ahti 1981), yet because of cold temperatures, the growing conditions remain moist. Slowly growing trees are relatively small, and forest canopies are sparser and more open than in the south (Kersalo and Pirinen 2009). Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) Karst.) most often dominate the canopy in European northern boreal forests. Downy birch (*Betula pubescens* Ehrh.) and its subspecies mountain birch (*B. pubescens* ssp. *czerepanovii* (N.I.Orlova) Hämet-Ahti) are also common and may be the dominating tree species of a forest site. The understory vegetation typically consists of a layer of mosses and lichens (such as splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.), Shreber's big red stem moss (*Pleurozium shreberi* (Brid.) Mitt.), and *Polytrichum* moss (*Polytrichum* Hedw.); *Cladonia* lichen (*Cladonia* P. Browne), Iceland moss (*Cetraria islandica* (L.) Ach.), and a layer of ericaceous shrubs (such as crowberry (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher) and *Vaccinium* spp. (L.)). The herb and grass layer is generally species-poor, with wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.), hairy wood-rush (*Luzula pilosa* (L.) Willd.), and arctic starflower (*Trientalis europaea* L.) being common examples (Hotanen et al. 2008).

In northern regions, reindeer husbandry is an important livelihood. Reindeer graze freely in many areas, which can influence the number of broadleaved trees, particularly their seedlings and saplings (Kreutz et al. 2015). Lichen biomass and coverage have drastically decreased in areas where reindeer husbandry is carried out in Finland. Bryophytes have replaced many lichen species in forests where reindeer trampling and grazing occur (Väre et al. 1995; Susiluoto et al. 2008; Akujärvi et al. 2014). The forests are also used in multiple other ways. Large areas are protected, and despite the slow growth of trees, forests are used commercially. The recreation value of both commercial and protected forest areas is high. Plenty of hiking routes run through vast regions, and berry picking and hunting are also important forms of forest usage.

Northern Finland, and the northern forests, may experience alterations in the future because of land-use changes. Northern Finland has many mines along with potential places for establishing new mines. One of the promising ore deposits is a phosphate massif, which lies in Sokli, eastern Lapland. The Sokli phosphate ore consists mainly of apatite [ $\text{Ca}_5(\text{PO}_4)_3\text{F}$ ] (Vartiainen and Paarma 1979), commonly used as an ingredient of phosphorus (P) fertilizers. Plans to open up a mine in Sokli have been alternating since the 1960s. Sokli is close to the Värriö Strict Nature Reserve, a protected area, where e.g. biological and air quality measurements have been conducted for decades. Sokli and Värriö are remote locations, and the air in the region is generally clean with barely any signs of pollution (Ruuskanen et al. 2003). The nearby Kola Peninsula in Russia is heavily industrialized with

non-ferrous metal smelters of mainly nickel and copper (at Monchegorsk, Nikel, and Zapoljarnij), iron mines and mills (at Kovdor and Olenegorsk), apatite mines (at Apatite and Kirovsk), and an aluminum smelter (at Kandalaksha) (e.g. Paatero et al. 2008). The ecosystems surrounding the industrial plants are severely polluted, and e.g. forests in the immediate vicinity of the smelters in Monchegorsk have been completely destroyed and replaced with so-called industrial deserts (e.g. Tikkanen 1995; Paatero et al. 2008). During the last decades, the production rates have decreased and many improvements have been conducted to reduce aerial pollution (gaseous sulfur dioxide and nitrogen dioxide and particle-bound metals such as arsenic, nickel, and copper) from the industry (Paatero et al. 2008). Nevertheless, the industry in Kola is still a source of pollution to the Peninsula and to some extent to Finnish Lapland. If the wind blows from the direction of Kola, higher quantities of pollutants are detected in the air at Värriö. However, this only happens occasionally and temporarily (Ruuskanen et al. 2003; Kyrö et al. 2014). The Sokli phosphate mine would be an open-pit mine (Pöyry Environment 2009). Such mines can cause the aerial deposition of phosphates and heavy metals into surrounding ecosystems (Reta et al. 2018). The material from the mine would be transported elsewhere by trucks for further processing (Pöyry Environment 2009). Thus, traffic pollution in the region would increase remarkably compared to the current situation.

In addition to land-use change, climate change affects the northern region of Finland. Climate change is predicted to be stronger and faster in northern latitudes than in the more southern locations (Kurtz et al. 2008; Hartmann et al. 2013). The reason for this is a process called Arctic amplification, which is a characteristic feature of the Earth's climate system and is expected to become stronger in upcoming decades (e.g. Serreze and Barry 2011). Because of Arctic amplification, the temperature rise in the Arctic (67° N to 90° N) is expected to be approximately 2 °C higher than elsewhere on the globe (Hartmann et al. 2013). Several other places in addition to Sokli in northern Finland have ore deposits, where new mines are being planned. Thus, large-scale changes due to land use and climate are expected to occur in the northern boreal region of Finland in upcoming decades. To be able to predict and be prepared for such changes, it is of utmost importance to assess what the baseline situation is.

## 1.2. Soil nutrients and their interactions with vegetation and atmosphere

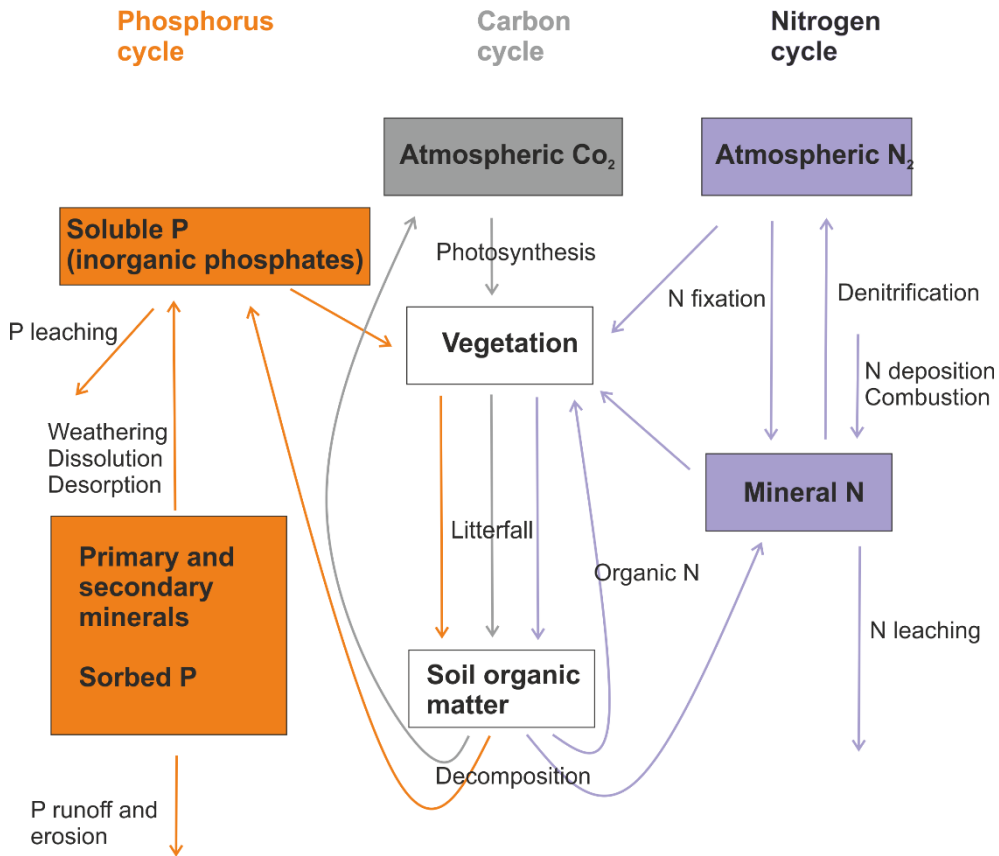
Plants need many nutrients for growth and maintenance, but the most important ones are usually nitrogen (N) and P, whose shortages can limit growth (Koerselman and Meuleman 1996). Boreal forests on mineral soils are generally limited by N (Tamm 1991), and tree growth usually increases when fertilized with N (Saarsalmi and Mälkönen 2001). Atmospheric deposition of N can act as a fertilizer in boreal forests (e.g. Korhonen et al. 2013). The annual N deposition to forests is 3–4 kg/ha in southern Finland and 1–2 kg/ha in northern Finland. These are low values compared to Central and Southern Europe, where the annual deposition of N can, at its highest, be as much as 30 kg/ha (Dirnböck et al. 2013). Excess amounts of nutrients have been linked with a decreased number of plant species in polluted regions experiencing heavy atmospheric N deposition (Dupré et al. 2002; Dirnböck et al. 2014). Plants use N for building up proteins (Marschner 1995). According to current knowledge, plants can directly utilize only certain forms of N. These forms are inorganic ammonium ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ) (e.g. Marschner 1995; Kielland et al. 2007), and organic amino acids (Kielland et al. 2007; Näsholm et al. 2008). These forms are available only in limited amounts in soil, and most of the N is bound in organic material (Marschner 1995).



Some plants, for example legumes, have specific nodules in their roots, with bacteria that can fix  $N_2$  directly from the atmosphere (Marschner 1995).

Single limitation by P in boreal forests on mineral soil has not been detected, but P limitation is possible on boreal peatlands due to slow mineralization (Brække and Salih 2002; Moilanen et al. 2010) and poor access to the underlying mineral soil (Shaver et al. 1998). Soil also holds P tightly, and very often it is the least mobile major nutrient for plants. Plants can take up P mostly as inorganic phosphates (Pi)  $H_2PO_4^-$  and  $HPO_4^{2-}$ , also called soluble P. Soluble P is derived from primary minerals (e.g. apatite) by weathering, secondary minerals (e.g. Ca and Fe phosphates), via dissolution, and from P sorbed on mineral surfaces (e.g. clay, carbonates, Fe, and Al oxides) via desorption. Additionally, P is mineralized from decomposing organic matter (Marschner 1995; Hinsinger 2001). Plants need P particularly during their early development, and use it in various processes such as photosynthesis and respiration. Plants that are able to fix  $N_2$  directly from the atmosphere need P for N fixation. Insufficient P causes problems with leaf development, and the number and size of leaves in a plant suffering from P deficit remain small (Marschner 1995; Raghothama 1999). Phosphates also act as building blocks for several important metabolites such as adenosine triphosphate, phospholipids, and nucleic acids (Marschner 1995; Raghothama 1999; Vance et al. 2003). Thus, P deficiency is a strongly limiting factor for plant growth even in otherwise favorable conditions. The co-limitation of N and P is common in many types of forests, and the ratio of these two nutrients is generally very important worldwide (Vadeboncoeur 2010; Augusto et al. 2017). For example, the addition of NP fertilizer to a temperate forest site in southern Sweden led to a doubling of vascular plant species richness (Hedwall et al. 2017). This effect was only seen when N and P were added together.

Nutrient availability in soil and the utilization of nutrients by plants are critical information for understanding processes in forest ecosystems (Merilä and Derome 2008). Understory vegetation, soil nutrients, and the local climate are important parts of a forest ecosystem and connect with each other in several ways. For example, soil nutrients and the climate affect vegetation species composition, and the growth and chemical composition of the vegetation. Species composition concurrently interacts with soil nutrients, as e.g. the mineralization rate of carbon (C) or N can vary under different plant species (Vinton and Burke 1995). While nutrient release in current conditions in northern boreal forests is slow, increased soil temperature induced by a warmer climate may speed up the processes in the future. Faster decomposition rates may increase the mineralization of both N and P from dead organic material. Climatic factors may affect the release of N more than P, at least in places where P availability is more dependent on the parent material of soil and landforms (Augusto et al. 2017). The global cycles of N, P, and C are interconnected (Figure 1), and changes in one can cause variation in the others, and thus re-shape vegetation. Understory vegetation in northern or high-altitude regions has already undergone changes, as increased temperature has caused the expansion of shrub cover in subarctic mountains in Sweden (Havström et al. 1992; Wilson and Nilsson 2009), high Arctic heath in Svalbard (Havström et al. 1993), Arctic tundra in Alaska (Chapin III et al. 1995; Hobbie and Chapin III 1998; Sturm et al. 2001) and elsewhere in the Arctic (Dormann and Woodin 2002; Walker et al. 2006), meadows in the Rocky Mountains (Harte and Shaw 1995), and dwarf shrub heath in Iceland (Jónsdóttir et al. 2005). An increase in growth is often linked with the amount of available nutrients, which are crucial for growth (Jónsdóttir et al. 2005; van Wijk et al. 2003).



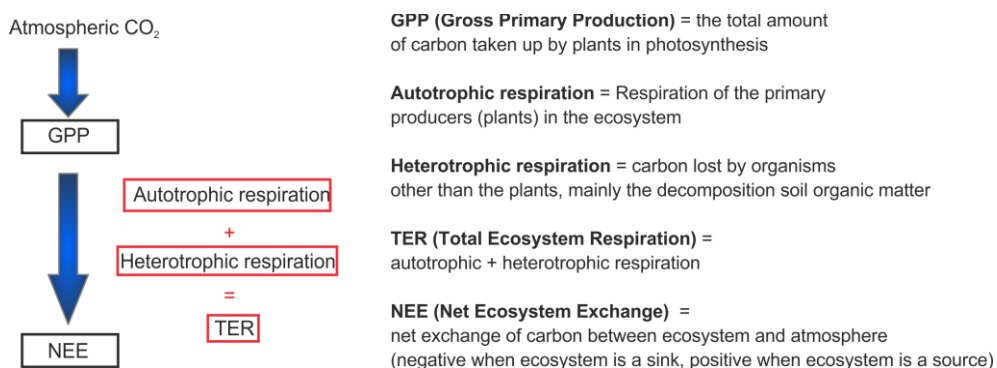
**Figure 1.** The global biogeochemical cycles of phosphorus (P, orange), carbon (C, gray), and nitrogen (N, purple) are interconnected. Modified from Llado et al. 2017.

### 1.3 Forest-atmosphere interactions and climate change

The importance of forests in the global C cycle is undeniable. Forests form both a notable sink of atmospheric C along with a C storage. A sink of C is a reservoir, which binds more atmospheric C than it releases. A C source is the opposite; a reservoir that releases more C than what it stores. A C storage is an entity that sequesters atmospheric C, such as living and dead plant biomass and soil. In boreal forests, the largest C storage lies in the soil (Pan et al. 2011) due to slow decomposition rates. Soil texture and nutrient availability affect how efficiently forests can bind atmospheric carbon dioxide ( $\text{CO}_2$ ). The understory vegetation may have an important role in the C dynamics of a forest, especially if the canopy is sparse (Kulmala et al. 2011; Hari et al. 2013) such as in northern boreal forests. The gross primary production (GPP) of the understory in the boreal forest ecosystem may be as much as 60% of the GPP of the whole site (Ikawa et al. 2015). Gross primary production basically equals the photosynthesis of the forest site, as it is the total amount of  $\text{CO}_2$  taken up by plants during photosynthesis (Figure 2). In addition to photosynthesis, plants also respire in a process that

is inverse to photosynthesis. Plant respiration is called autotrophic respiration, which can be divided into maintenance respiration and growth respiration. Maintenance respiration depends on biological activity, which increases with temperature and is highest in tissues with high metabolic rates (Ryan 1991). Growth respiration is proportional to growth (Amthor 2000). When it is dark, plants only respire, while they both respire and photosynthesize when light is available. Temperature drives both photosynthesis and respiration, but respiration is more sensitive to temperature changes than photosynthesis is (Ryan 1991). The balance between respiration and photosynthesis may be modified by climate change, as the same environmental drivers cause different impacts (DeLucia et al. 2007).

In northern boreal forests, the current growing conditions have prevailed for many millennia. However, notable changes will likely occur in this area because of climate change. Rising mean annual temperatures, prolonged growing seasons, and increased precipitation rates are expected and have already happened in northern regions (e.g. Hartmann et al. 2013; Peñuelas et al. 2020). In addition to these more general changes in growing conditions, extreme weather events are expected to become more frequent than currently (e.g. Beniston 2004; Hartmann et al. 2013). Such events include drought, heat, heavy rain, and frost in the summertime, which may all have negative impacts on the forest ecosystems and their CO<sub>2</sub> and water (H<sub>2</sub>O) exchange. Water also circulates between the vegetation and atmosphere. While taking in CO<sub>2</sub> through their open stomata, plants simultaneously release H<sub>2</sub>O to the atmosphere. To replace the resulting loss, plants need to absorb H<sub>2</sub>O from the soil. The release of water to the atmosphere is called transpiration. The term evapotranspiration (ET) is used when plant transpiration is combined with the evaporation of water from different surfaces in the forest.



**Figure 2.** The terms and concepts related to the carbon dioxide (CO<sub>2</sub>) exchange between ecosystem and the atmosphere. (Modified from Kallioikoski et al. 2019).

Scots pine, Norway spruce, and their understory vegetation grow in different nutrient and hydrological conditions and may therefore react differently to forthcoming changes. Norway spruce is known to be more prone to drought than Scots pine (e.g. Lebourgeois et al. 2010; Lebourgeois et al. 2012; Eilmann and Rigling 2012; Lévesque et al. 2013; van der Maaten-Theunissen et al. 2013; Baumgarten et al. 2019), and also more sensitive to frost than Scots pine (Lundmark and Hällgren 1987; Linkosalo 2014). Frost during the growing season can damage the leaves and reduce their greenness (Gu et al. 2008; Linkosalmi et al. 2016). Droughts are uncommon in northern regions; instead, precipitation and soil moisture are generally considered sufficient for growth. However, a tree-ring study from a northern boreal forest in Finland showed that Scots pine and Norway spruce growth had decreased during dry years (Aakala et al. 2018). The same happened with white spruce (*Picea glauca* (Moench) Voss) in Alaska (Barber et al. 2000; Wilmking et al. 2004). At least further south, drought has apparently caused remarkable changes in CO<sub>2</sub> flux rates. During a drought in 2003, GPP decreased in many parts of Central and Southern Europe (Ciais et al. 2005) and Northern Europe was also affected during a drought in 2006. For example, the 2006 drought led to the GPP and ET rates of a Scots pine forest to decrease strongly in southern Finland (Gao et al. 2016; Gao et al. 2017). When the climate warms, such phenomena could also occur further in the north. In many forest ecosystems, the respiration rate of plants (i.e. autotrophic respiration) increases with rising temperature, which may cause negative impacts on the C balance of plants (Jones et al. 1998). The decomposition of organic matter, i.e. heterotrophic respiration, also depends on temperature (Davidson and Janssens 2006). High temperatures may amplify the rate of decomposition and turn northern soils from a C sink to a C source (Crowther et al. 2016). However, certain soil microbes suffer in dry conditions, and drought may inhibit their functioning (Moyano et al. 2013; Sierra et al. 2015). Nevertheless, some changes will likely occur in decomposition rates, possibly reducing ecosystem respiration. These changes may also affect the release of soil nutrients, which in turn affects vegetation, followed by variation in CO<sub>2</sub> exchange.

## 2. AIM OF THE STUDY

In this dissertation, I aim to analyze and characterize the baseline status and the future aspects of northern boreal forest vegetation in Finland to assess the resilience of structure and CO<sub>2</sub> sink in changing conditions. My objectives are to 1) identify the connections between soil N and P content and forest vegetation, 2) quantify the relationship between all forest vegetation and atmosphere considering the CO<sub>2</sub> flux between them, and 3) based on the above, discuss how climate change will affect northern boreal forests in terms of vegetation, nutrient cycling, and CO<sub>2</sub> flux dynamics.

More specifically, with the help of the three sub-studies included in this dissertation, I aim to answer the following questions:

**Question 1 (Q1):** What is the relationship of soil total N and P content with vegetation cover composition in a northern boreal forest located near a phosphate massif?

**Question 2 (Q2):** What is the role of understory vegetation in the CO<sub>2</sub> flux dynamics of a northern boreal Scots pine forest?

**Question 3 (Q3):** How resilient are the CO<sub>2</sub> exchange rates of northern boreal forests to extreme weather events and climate change?

**Question 4 (Q4):** Will the nutrient dynamics and the composition of plant species change in northern boreal forests in the future?

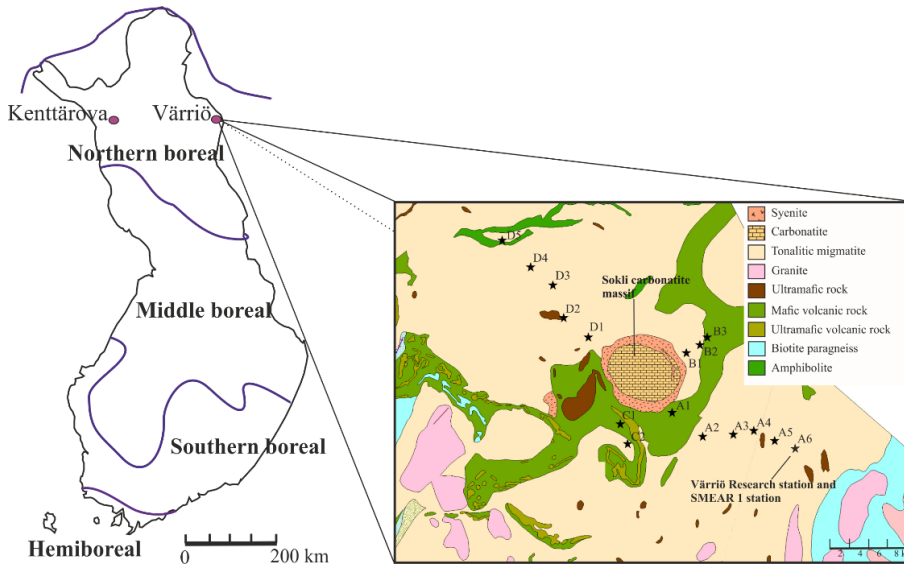
For this purpose, I studied three forest areas in Finnish Lapland: the surroundings of the Sokli phosphate massif near Värriö (eastern Lapland) (Article **I**) and a Scots pine site in Värriö both alone (Article **II**) and in comparison with the Kenttäröva Norway spruce site in Pallas (western Lapland) (Article **III**).

### 3. METHODS

#### 3.1 Study sites

All three articles used data measured at or in the surroundings of Värriö Subarctic Research Station (67° 44' N, 29° 36' E) in eastern Lapland in Finland. In article **I**, we had 16 study plots (Figure 3), which were located in the surroundings of Sokli phosphate ore mine (67° 48' N, 29° 16' E). Each of these plots was 30 × 30 m<sup>2</sup> in size, and they included twelve sub-plots per plot for observing the understory vegetation and coring soil samples. These plots had Scots pine, Norway spruce and downy birch as the main tree species. Some plots had a mixed composition of all three species. In article **II**, we used data from the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR I station, 67° 46' N, 29° 35' E), which is located at the Värriö Research Station. The mean annual temperature and mean annual precipitation are -0.5 °C and 601 mm, respectively (Pirinen et al. 2012). The site is a Scots pine forest located 400 m above sea level. The understory vegetation at the SMEAR I station is very typical for the region: a combination of mosses and lichen, such as Schreber's big red moss, broom fork-moss (*Dicranum scoparium* Hedw.), and reindeer lichen (*Cladonia rangiferina* (L.) F. H. Wigg.), along with dwarf shrubs, most commonly bilberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), and crowberry. Soil type is haplic podzol with sandy tills (FAO 1988), similarly to the soils at the plots in article **I**. The understory vegetation of the plots in article **I** was relatively variable and will be discussed in section 4.

In article **III**, we used data from SMEAR I, and Kenttäröva forest (67° 59' N, 24° 15' E), which is located at the Pallas Atmosphere-Ecosystem Supersite hosted by the Finnish Meteorological Institute (FMI) (Figure 3). The mean annual temperature at the site is -1.0°C and mean annual precipitation sum is 521 mm (Pirinen et al. 2012). The Kenttäröva site is a Norway spruce forest with some downy birch, Eurasian aspen (*Populus tremula* L.), and goat willow (*Salix caprea* L.) growing as mixed species. The forest is located 347 m above sea level on a hilltop plateau, which is circa 60 m above the surrounding planes (Aurela et al. 2015). The understory at Kenttäröva mainly consists of mosses, such as Schreber's big red moss, splendid feather moss, and rugose fork-moss (*Dicranum polysetum* Sw.), and dwarf shrubs bilberry, crowberry and lingonberry. Soil type is podzolic till (Aurela et al. 2015).



**Figure 3.** The boreal subzones (according to Hämet-Ahti 1981) and locations of Värriö pine site and Kenttäröva spruce site on the left. The study plots used for article I are shown in the geological map.

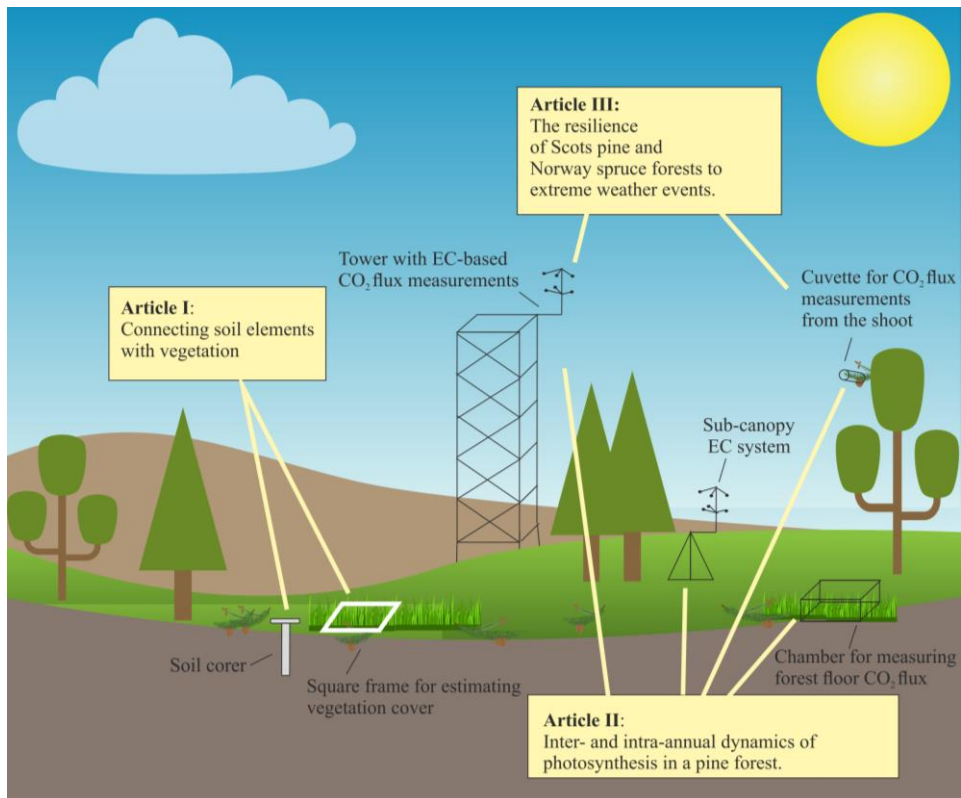
### 3.2 Measurements and laboratory analyses

#### 3.2.1 Field measurements (Articles I–III)

The field measurements focused on the features of vegetation and soil nutrient contents, and momentary fluxes of  $\text{CO}_2$  and  $\text{H}_2\text{O}$ . Figure 4 illustrates the three articles and some of the methods used in them. The understory vegetation survey was conducted by setting a square frame of  $1\text{ m}^2$  onto the ground, recording all the plant species within the frame, and visually estimating their approximate projection cover (percentage of surface). Four soil samples were taken next to each vegetation square with a corer (diameter 5 cm), so that the maximum distance of the sample was 1 m away from the square (Liski 1995). The maximum depth of the samples was approximately 15 cm, as the soil layers were very shallow, and in places it was hard to core the samples because of the rocky soil. Due to lack of laboratory space and resources at the site, the soil samples were divided into different soil horizons directly after sampling. We used the same definitions for the soil horizons as Köster et al. (2014). Thus, the four soil horizons were F (litter layer), O (humus), A (eluvial layer), and B (illuvial layer). After separation of the horizons, we had four samples of each horizon from each sub-plot. These were pooled to form one composite sample per horizon per sub-plot. In the study, we also measured the heights and diameters (diameter at a height of 1.3 m) of all trees inside the  $900\text{-m}^2$  area and took needle/leaf samples from conifers (five trees per species) and birches (fresh and litter leaves). More detailed information of the study setup and fieldwork is in article I.

Carbon and  $\text{H}_2\text{O}$  flux measurements (II and III) were based on the eddy covariance (EC) method. The necessary devices for EC were set up in towers above the canopy at both the SMEAR I and Kenttäröva sites. The scale in these measurements is the whole ecosystem,

thus the trees, understory, and soil were all included. Article **II** included, in addition, flux data from a sub-canopy EC system and soil chambers from Värriö, while article **III** included cuvette (shoot chamber) flux data from Värriö and EC data from the Kenttäröva site in Pallas. Especially in studies **II** and **III**, we utilized data from meteorological measurements, mainly from the FMI measurement sites at Värriö Subarctic Research Station and at Alamuonio near Kenttäröva. A detailed explanation of the flux and meteorological measurements can be found in articles **II** and **III**.



**Figure 4.** The three articles in this thesis, and their most important measurement methods.

### 3.2.2 Laboratory analyses (Article I)

The soil samples from mineral soil layers A and B were air-dried and the samples from the organic F and O layers were dried at 60°C for 48 hours on-site. The samples were stored as dried for a couple of months, after which the mineral soil layers were sieved with a 2-mm sieve, and the organic samples were milled before storing them again in a dry place for further analyses. The needle and broadleaf samples were dried at 60°C for 48 hours. After this, the samples were stored in a dry place for further analyses. Later on, all the samples were wet combusted (details in article I) and the resulting extracts were analyzed for their total elemental concentrations (P) by inductively coupled plasma optical emission spectrometry. I also analyzed total C and N directly from the sieved and milled soil, and leaf and needle samples with an element analyzer, which uses a high-temperature combustion method with subsequent gas analysis of C and N (VarioMax, Elementar Analysensysteme GmbH, Germany). I analyzed pH from the O layer from a suspension where the sample was mixed with ultrapure water. Details of the analyses can be found in article I.

### 3.2.3 Data analyses (Articles I–III)

In article I, we utilized linear mixed-effect models for quantifying which factors (dominant tree species, tree age, rock parent material, soil layer) affect the soil nutrient content the most. We used non-metric multidimensional scaling for ordinating the plots based on their average understory vegetation cover (% of soil surface) (Minchin 1987). We then fit vectors of different environmental factors (nutrient contents in the humus layer, volume of birch) to see their relationship with the ordination pattern. We also used one-way analysis of variance (ANOVA) to compare the needle nutrient contents in different age groups and between the research plots. All these analyses were performed in R programme 3.4.3 (R Development Core Team, 2017), and the detailed information with all the used R packages are in article I.

Article II describes the data processing and calculations needed for the EC data in articles II and III. This processing includes gap-filling of the data by modeling the photosynthesis and respiration with a set of parameters derived from available observations together with measured temperatures of air and soil. We additionally used the optimal stomatal control model (Hari and Mäkelä 2003; Kolari et al. 2007) and the Stand Photosynthesis Program (Mäkelä et al. 2006) to help estimate the photosynthesis of a canopy from shoot flux data. The downscaled GPP of the understory was calculated as a difference between the GPP of the whole ecosystem (from EC) and the estimate of canopy photosynthesis. Understory photosynthesis was also calculated in another way by upscaling it from modeled species-specific photosynthesis rates of vascular plants. From the difference of the EC-derived GPP and the upscaled photosynthesis of the understory, we obtained another estimate for tree canopy photosynthesis. We thus had upscaled and downscaled versions for both the canopy and the understory photosynthesis. We used data from 2012–2015 in article II.

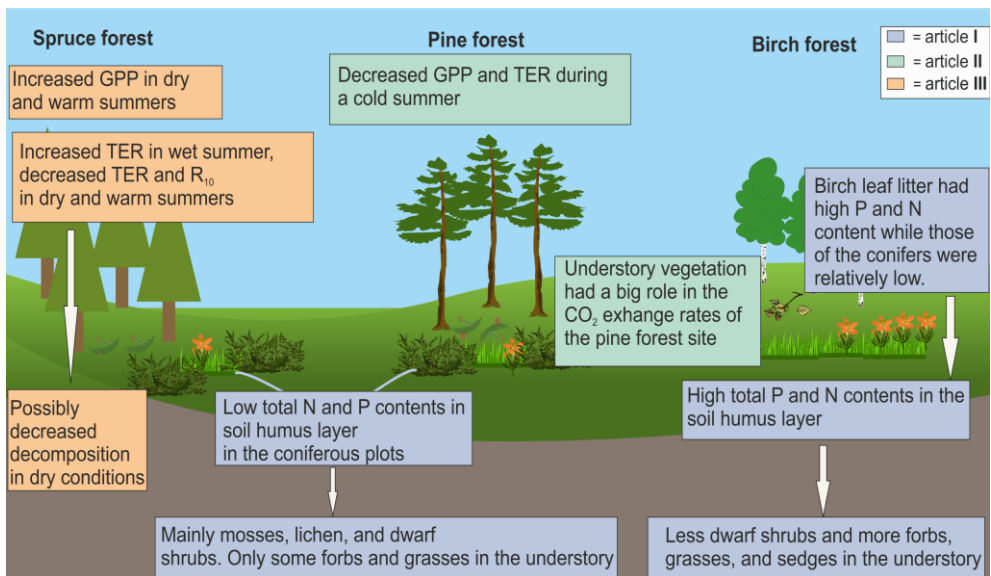
In article III, we used long-term meteorological data (from 1981–2010) and compared it with meteorological data from the study years. These study years were 2012–2018 for Värriö pine forest and 2003–2013 for Kenttäröva spruce forest. We calculated  $R_{10}$  and  $P_{1200}$  (normalized respiration at a constant temperature of 10°C and photosynthesis at constant photosynthetically active radiation (PAR) of 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively) from the EC data and photosynthetic capacity  $\beta$  from the pine shoot flux data. We also calculated the ratio of ET/vapor pressure deficit (VPD). We utilized one-way ANOVA to compare summertime



values of TER, GPP,  $R_{10}$ , and  $P_{1200}$  between the study years. A more detailed description of the calculations is in article III.

## 4. RESULTS AND DISCUSSION

In chapter 4.1, I will answer **Q1–Q3** by going through the most important results of articles **I–III** (illustrated in Figure 5) and discussing them in relation to the existing literature. In chapter 4.2, I discuss what is suggested to happen to northern boreal forest vegetation in the future (**Q4**).



**Figure 5.** The main results of the articles in this dissertation. Box color describes the source article. Data for spruce forest were from 2003–2013 and for pine forest from 2012–2018.

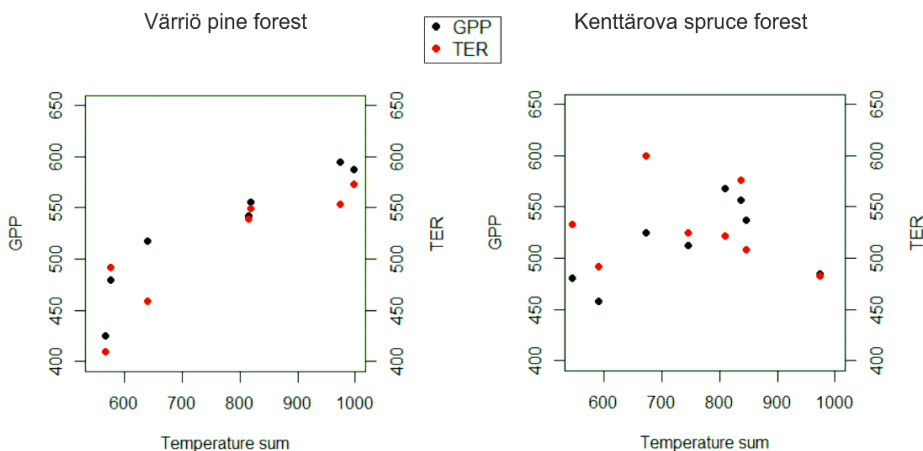
#### 4.1 The baseline status of soil-vegetation-atmosphere interactions in northern boreal forests (Q1–Q3)

My first research question (Q1) dealt with the connection of soil N and P contents with vegetation cover in northern boreal forests near a phosphate massif. The contents of these nutrients are important for forest vegetation, especially in the organic layers of soil where the roots of the understory vegetation grow. Most nutrient studies from boreal forests have focused on N, because of its growth-limiting role. Several fertilization studies have shown that addition of N changes the understory species composition in boreal forests (Mäkipää 1999; Strengbom et al. 2002; Gundale et al. 2014). Similarly, Salemaa et al. (2008) found that the number of vascular plant species (grasses and forbs) in boreal forests increased together with increasing N content in the organic soil layer. Their study covered several forest sites across Finland. However, in Arctic, subarctic, and alpine tundra ecosystems, P may co-limit or limit plant production (Shaver and Chapin 1995; Aerts and Chapin 1999; Seastedt and Vaccaro 2001; Hobbie and Gough 2002; Soudzilovskaia et al. 2005; Giesler et al. 2012). Both the weathering and mineralization of P may be restricted because of the cold climate in the tundra (Stark 2007). In addition, certain microorganisms in tundra soil need P and thus may compete with plants in P uptake (Jonasson et al. 1999). Arnesen et al. (2007) found that the availability of P in the soil together with pH and carbonate contents correlated the best with alpine vegetation on exposed rocky habitats in northern Norway. They found that the diversity of vascular plants increased with higher P availability. We found evidence of the importance of soil P content in northern boreal forests, albeit our site was very special because of the Sokli carbonatite massif (I). Our results showed that both N and P contents in the humus layer were important in explaining the community composition of understory vegetation in northern boreal forests (Figure 5). Humus P content seemed even more important than N content, and the coverage (% of surface) of species preferring more fertile growing conditions (forbs, grasses, and sedges) increased almost linearly with it. Salemaa et al. (2008) also found that extractable soil P had a higher importance for vegetation patterns in the north than in southern Finland, which supports our finding.

The understory vegetation in the plots of article I consisted of common Finnish forest species (Reinikainen et al. 2000). At most plots, the vegetation cover was typical for the most common forest site types in the region (Cajander 1909, 1949; Hotanen et al. 2008). The understory consisted of mosses (e.g. Schreber's big red stem moss), lichen (e.g. *Cladonia* spp.) and dwarf shrubs (e.g. bilberry, crowberry), whereas Norway spruce or Scots pine were the dominating tree species. However, in some plots downy birch was the dominant tree species and the understory had a higher number and coverage of forbs, grasses, and sedges (such as wood small-reed (*Calamagrostis epigejos* (L.) Roth), sedges (*Carex* L.), Arctic raspberry (*Rubus arcticus* L.), and hairy wood-rush). These plots also had high N and P contents in the humus layer. Although the needle and broadleaf contents of N and P did not differ significantly between the plots, tree species was important for the nutrient dynamics of the research plots. The results of the mixed-effect model showed that the dominating tree species (Scots pine, Norway spruce, or downy birch) together with soil layer (P content in the different layers) were the most important factors explaining soil P content. When we inserted birch as the dominant tree species and F layer P content into the model, it explained 45% of the total soil P content (data from all layers were considered). This was the most explanatory model of all. For soil total N content and soil C:N ratio in all layers, soil horizon was the most important factor explaining 20% of both. The best estimates of N were obtained with F as the soil horizon. Our results suggest that birch, with its high annual input of leaf

litter, forms an important source of P to the soil. Supporting this, experimental studies have reported that adding birch leaf litter increased the total and available content of P in the soil (Rinnan et al. 2008; Sorensen and Michelsen 2011).

What comes to **Q2**, our results (**II**) found that the role of the understory vegetation in stand photosynthesis was high at the Scots pine site. It accounted for 43% to 49% of the annual whole ecosystem photosynthesis, depending on the year. A high proportion (61%) of understory in the stand photosynthesis was also reported from an Alaskan black spruce (*Picea mariana* Mill.) forest with an open canopy (Ikawa et al. 2015). Studies from more southern boreal forests with higher canopy covers have reported understory shares ranging from 10% to 20% (Swanson and Flanagan 2001; Kolari et al. 2006; Ilvesniemi et al. 2009; Bergeron et al. 2009). Differences also exist between the compartments of a forest site regarding their annual dynamics. The canopy photosynthesis rate in the Värriö Scots pine forest began increasing about a month before snowmelt (**II**). Thus, the understory was still under snow cover when the canopy experienced its spring awakening. Many models related to primary production do not take snow cover into account, and for that reason, may not accurately estimate the production of forests with open canopies. The Värriö pine forest was a CO<sub>2</sub> sink from around mid-May to early September. Rainy days sometimes caused the forest to turn into a source of CO<sub>2</sub> also during the summer. This occurred especially in summer 2015, when the weather was cloudy and rainy throughout the summer and the PAR level was too low for efficient photosynthesis. In the short term (2012–2015), GPP seemed to have a higher response to temperature sum than TER (**II**). This trend remained similar, although it evened out when three more study years (2016–2018) were included (Figure 6). These findings are similar to previous studies (Law et al. 2002, Mäkelä et al. 2008). Contrariwise, such a clear connection between temperature sum and GPP and TER did not exist in Kenttäröva spruce forest (Figure 6). Other factors, such as soil drying, may restrain GPP and TER once the temperature sum is high enough.



**Figure 6.** Annual GPP and TER ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ) over cumulative temperature sums (the unit is  $^{\circ}\text{C}$  and a  $5^{\circ}\text{C}$  threshold was used) from Värriö pine forest and Kenttäröva spruce forest site. Some data were missing from Kenttäröva and thus the years 2007, 2009, and 2010 are missing from the figure.

It is normal for northern boreal forests to experience summer conditions varying from cold to relatively warm and everything in between. This is visible, for example, in the variation of temperature sums between the years in Värriö and Kenttäröva (Figure 6). As we discovered (**II** and **III**), the variation in CO<sub>2</sub> fluxes between the forests and atmosphere can be high between the years. Some of the summer seasons at our Scots pine and Norway spruce sites were so different from the long-term average (30 years of data) in terms of temperature or rainfall, that they fulfilled the IPCC definition for statistically extreme (Seneviratne et al. 2012) (**III**). The statistical definition is a good starting point for defining extreme events, but sometimes ecosystems may respond extremely even though the statistical criteria are not met (Gutschick and BassiriRad 2003; Smith 2011). In our findings, only the Värriö pine forest had extremely warm or dry summers in statistical terms. However, the effects of warm and dry conditions in both the measured and modeled CO<sub>2</sub> flux rates were more visible from the Kenttäröva spruce forest. Kenttäröva spruce forest seemed less resilient against extreme events than the Värriö pine forest. Both the measured and modeled respiration (TER and  $R_{10}$ , respectively) rates decreased during a period of July–August in the dry and hot years compared to other study years (Figure 6). The GPP, on the other hand, increased during the dry and warm years in both forests (**II** and **III**). For this reason, and because TER significantly increased during a wet summer, the decrease of TER values during dry and warm summers was apparently caused by lowered decomposition of soil organic matter. This implies that predictions estimating that all northern forest soils will turn into C sources because of climate warming seem slightly exaggerated. The H<sub>2</sub>O flux rates from forests also depend on temperature. Some climate models have predicted that amplified ET may outweigh the predicted increase in precipitation and cause intermediate drying of soil in boreal forests (Ruosteenoja et al. 2017). Our study did not find evidence of anything like this, as the H<sub>2</sub>O fluxes or the ratio of ET/VPD of the spruce or pine forests did not differ between years (**III**).

Cold spells may occur if a spring is warmer than usual and a frost follows after the vegetation has already started growing and photosynthesizing. Such cold spells have been found to cause remarkable damage to vegetation. In eastern US, a freezing period after an exceptionally warm spring led to crop plant mortality and severe damage to tree leaves (Gu et al. 2008). The greenness of plants was remarkably reduced. The vegetation in northern boreal forests is considered to be rather resistant towards coldness. After all, the growing conditions are relatively cold and the growing seasons short (e.g. Pirinen et al. 2012). However, a cold spell occurred around mid-summer 2014, which showed that reduced leaf greenness also occurs in the north (Linkosalmi et al. 2016). During this same cold spell in 2014, which lasted for 11 days in Värriö, we saw a temporary dip in the photosynthetic capacity  $\beta$  of pine shoots. When the cold spell was over,  $\beta$  increased together with temperature. This implies that the cold spell was either not harsh enough to cause severe damages or the vegetation was very resilient towards such spells. A cold summer reduced the GPP and TER rates of the Scots pine forest compared to other study years. The year following the cold one was extremely warm, and the forest photosynthesized with record high values. This implies that the cold summer did not damage the vegetation, for example the buds, which form in fall. Similarly, photosynthesis and respiration of the spruce forest returned to their average levels after the dry years, implying that at least the trees were not harmed (**Q3**).

## 4.2 Northern boreal forest vegetation in the future (Q4)

Northern forest ecosystems are often described as vulnerable to climate change, which is amplified at high latitudes (Kurtz et al. 2008; Hartmann et al. 2013). Local variation in the consequences of climate change may be high, and most forest processes are interconnected. Thus, it is not easy to say exactly what kind of effects climate change will cause on forest vegetation. However, several experimental and modeling studies have tackled the issue, and their results shed some light to what may take place in the future. According to simulations related to the effects of climate change on forest biodiversity in Finland (Kellomäki et al. 2005, 2008), species richness (number of species) may increase in the north of the country. This occurs if decomposition of organic matter increases and the release of nutrients speeds up, leading to increased productivity of forestland. On the other hand, species that currently grow at high latitudes seem to suffer the greatest losses (Skov and Svenning 2004) and shifts in tree species and their compositions are expected (Sykes et al. 1996; Thuiller 2003). According to other modeling predictions (Bakkenes et al. 2002), over 90% of the currently occurring higher plants should maintain their distribution in a 50-year time span, although regional extinctions may occur (Sætersdal et al. 1998). Specialist species will likely suffer and those that are able to grow in various conditions will benefit from the situation. Next, I will take a closer look at the reasons causing the changes in vegetation that I described in this section.

Warmer temperatures may affect vegetal growth and the CO<sub>2</sub> exchange between vegetation and the atmosphere. Northern boreal forest ecosystems are on the edge of the northern forest line and are generally considered to be sink-limited so that tree growth depends on temperature (Körner 2003). Previous studies have reported that with increasing temperature, forests in the north will likely benefit and increase their growth (e.g. Nemani et al. 2003; Boisvenue and Running 2006; Lindner et al. 2010). We showed that warm weather caused the forests at Värriö (II and III) and Kenttäröva (III) to photosynthesize at high rates. The results from article II also imply that the dwarf shrub-dominated ground vegetation of a Scots pine site begins photosynthesizing more when the temperature is higher.

Rising air temperatures can lead to warmer soil temperatures. This can cause higher microbial activity, faster decomposition rates, and nutrient circulation, as e.g. N mineralization should speed up in warmer conditions (Rustad et al. 2001; Robinson 2002). In certain cases, soil warming may decrease the amount of available soil water, which can hinder soil microbial activity and slow down decomposition rates (Sjögersten and Wookey 2004; Hicks Pries et al. 2013). As mentioned, this could have been the case in Kenttäröva spruce forest, where the slower decomposition rates may be one reason for the decrease in TER during warm and dry summers (III). In the course of climate change, the frequency of extreme weather events is expected to become higher than currently. We may thus expect more extremely warm summers, which may cause a decrease in TER, especially in northern Norway spruce forests. The understory species of spruce forests may be more susceptible to droughts than the species growing in Scots pine forests. For example, bilberry, which is very common in spruce forests, has been found to recover slower from drought than lingonberry, which is more common in pine forests and drier sites (Ganthaler and Mayr 2015; Palmroth et al. 2019).

Shrub cover increases in Arctic regions with a warming climate (Bret-Harte et al. 2001; Sturm et al. 2001; Walker et al. 2006; Park et al. 2016). Walker et al. (2006) observed that the height of graminoids, forbs, and shrubs along with the dominance of woody plants increased with warming at treeless high and low Arctic and alpine ecosystems. As several

studies have found, climate warming has, to some extent, corresponding effects on vegetation as nutrient addition. This is likely because it causes increased nutrient mineralization in some ecosystems. Increased N mineralization may in turn boost plant growth (Hobbie et al. 2002; Robinson 2002). For example, the production and biomass of woody shrubs increased after N and P fertilization at a moist tundra site in Alaska (Chapin et al. 1995; Chapin and Shaver 1996). In boreal forests, fertilizing with N is well known to increase volume growth and tree foliage biomass (Axelsson and Axelsson 1986; Sigurdsson et al. 2013; Lim et al. 2015; From et al. 2016). Canopy closure occurring because of larger tree leaf area leads to reduced light availability for understory species. The C uptake of understory species can change because of this, and the direction of the change varies between species, as Palmroth et al. (2019) recently discovered in a Norway spruce site in northern Sweden. In their study, an increase in the leaf area index of trees together with annual N addition decreased the C uptake of bilberry and lingonberry, while the C uptake of wavy hair-grass increased. Despite the decrease in C uptake of the most dominating understory species, the contribution of the field layer to stand photosynthesis did not decrease. This was because the mean annual biomass of wavy hair-grass, which has a high photosynthetic capacity (Kulmala et al. 2009), increased to almost three-fold compared to the original situation, which was enough to keep field layer photosynthesis at its original level.

Canopy closure may protect the understory vegetation from heat, and the microclimate under the canopy may be a more important driver for understory species dynamics than the underlying macroclimate (Zellweger et al. 2020). This suggests that the common temperature data measured from the meteorological stations (at about a height of 2 m, relatively open surroundings) are not the best possible data to be used when modeling or predicting the effects of climate change on understory vegetation. In certain conditions, so-called microrefugia may form for sensitive plant species. Microrefugia are small areas where the microclimate creates such conditions that a species can survive despite general growing conditions becoming unfavorable for its persistence (Ashcroft et al. 2010; Keppel et al. 2012). Such microrefugia, or the effects of a microclimate, are relatively poorly known in the boreal region. However, the local microclimates may apparently even out the effect of a rising mean annual temperature on understory vegetation (Zellweger et al. 2020), and some plants at the edge of their range margins can persist in microrefugia when surrounding conditions change (Greiser et al. 2019).

As mentioned, climate change can cause similar changes as fertilization in the nutrient status of a northern ecosystem. Peñuelas et al. (2020) recently reported that the foliar nutrient contents of several tree species have decreased with increased atmospheric CO<sub>2</sub> concentrations in Europe during 1990–2016. This had occurred elsewhere, except in the north, where foliar N, sulfur, and calcium contents increased over time and P contents remained similar. The increased nutrient contents in the north correlated with increased mean annual temperature and the following enhanced availability of N in the soil. Annual precipitation sums also increased in the north during the study period, unlike in more southern locations, where increasingly dry conditions were considered to hinder nutrient uptake by plants.

In northern Finland, Rousi et al. (2017) found that increased N mineralization can be one of the main ways for the predicted northwards movement of the tree line. Their study implied that, contrary to previous beliefs, trees can move long distances towards the north if the climate warms and soil fertility is high. The species may also spread to regions where it previously did not grow (Rousi et al. 2017). Birch species together with Scots pine are expected to become more dominant and replace Norway spruce in many places (Kellomäki

and Kolström 1992; Talkkari 1998; Kellomäki et al. 2001, 2005, 2008). Birch trees can be important for the nutrient circulation of a site (I), but also in other ways. For example, in northern Finland, mountain birch was able to facilitate Scots pine growth under its canopy despite the soil nutrient status (Mikola et al. 2018). Warmer temperatures may also cause changes in the elevational tree line, as Aakala et al. (2014) discovered in Värriö, where Scots pine has colonized on the tops of previously treeless fells during past decades. In addition to this newly organized distribution of an already existing species, new species may shift from more southern regions to the north. Plant species dynamics are very complex and many things can directly or indirectly alter species communities. For example, insect outbreaks are predicted to become more common with climate change. They can drastically decrease the photosynthetic rates of a forest, as observed in an outbreak of autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) in a mountain birch site in northern Sweden (Olsson et al. 2017). In Finland, these particular species occur in the northernmost part of the country, but other insects may cause similar damage elsewhere.

## 5. CONCLUSIONS

Northern boreal forests are located at their growth limits, making them vulnerable to large-scale consequences of climate change, such as shifting of vegetation zones. On the other hand, these forests are considered relatively resilient, although the term resilience is somewhat hard to define and confusing to many (see e.g. Nikinmaa et al. 2020). Nevertheless, northern forests are expected to recover well after short disturbances such as extreme weather events. In this dissertation, I studied the baseline status and the responses of northern boreal forest vegetation to climate change. Several studies have shown the importance of the relationship of soil N and boreal vegetation cover. So far, soil P in boreal forests has received relatively little interest compared to N, and most studies regarding P have concentrated on former agricultural lands (Peltovuori 2007; Soenne et al. 2008) or on peatlands (e.g. Moilanen et al. 2010). However, an increasing number of studies imply that soil P is also important for northern forest vegetation growing on mineral soil. In our study (I), the N and P contents of the humus layer largely explained the understory community compositions in forests. Understory vegetation may have a substantial role in the carbon dynamics of a forest site, as was the case at the Värriö Scots pine site (II). Extreme weather events had occurred both at the Scots pine and Norway spruce sites and caused temporary changes in CO<sub>2</sub> flux rates (III). These changes occurred more clearly in the Norway spruce site.

The studied forest ecosystems seemed to be rather resilient to climatic extremes that have occurred at the sites so far (III), meaning that they recovered quickly and the vegetation was not physically damaged. If extreme weather events become stronger or more frequent, as predicted, the cold spells or droughts may cause severe damage to forest vegetation. Annual plants may die as a result, while perennial plants maybe survive but could lose some of their biomass. Droughts also increase the risk of fires, which greatly modify forest vegetation. A warmer temperature is predicted to increase the mineralization and availability of nutrients, but warm and dry conditions may also slow down organic matter decomposition in some forest sites, which seemed to be the case in Kenttäröva spruce forest (III). The trees may photosynthesize more and begin growing better because of warmer temperatures, which is

what our results also suggested (**II** and **III**). If this happens for a long enough period, the forests may begin resembling forests that grow in the central or southern boreal zones. Forest canopies may become more closed, which causes shading and changes in vegetation species, leading to changes in the carbon flux dynamics of these forests. Canopy closure will also increase interception, which means that in addition to decreased light levels the understory vegetation may end up with less water (Palmroth et al. 2019). The change in forest microclimate caused by increased shading may also protect the understory species from changes in the macroclimate such as rising air temperature (e.g. Zellweger et al. 2020).

Local variation in the nutrient availability of ecosystems may naturally also occur in the future. Possible mining-related changes may affect nutrient availability in the Värriö region. Open pit mining can lead to aerial deposition of phosphate and heavy metals, which in turn could change the nutrient dynamics and plant communities on a local scale. The region currently receives very little pollution, with air concentrations increasing only occasionally when the wind blows from the Kola Peninsula. Unlike soil N, P is not so dependent on climatic factors directly, but relies more on soil parent material and landforms (Augusto et al. 2017; Deiss et al. 2018). However, as the P cycle is connected with the N cycle, alterations in the N cycle due to climate change could impact the P cycle. This in turn can lead to changes in photosynthesis rates along with other carbon, energy, and water cycling between ecosystems and the atmosphere. The possible aerial deposition from the mine could speed up the otherwise slow movement of P in the ecosystems and affect nutrient cycles and vegetation compositions. It could have similar effects as e.g. the greater increased leaf litter input caused by increased shrub cover. The combined effects of mining and climate change are nevertheless hard to predict. The current processes, interactions, and feedbacks between soil nutrients, vegetation cover, and the atmosphere in northern boreal forest ecosystems require more research to be able to forecast the future changes. The role of the understory vegetation and its annual cycle, which differs from that of the forest canopy, is crucial in northern forest ecosystems in terms of carbon exchange. Yet, this is poorly considered in climate modeling because of the lack in research on the topic. Many research gaps also exist concerning how microclimates vs. macroclimates interact with species communities in northern latitudes. In addition to the scientific community, entities responsible for nature conservation, forest management, and other land use management would all benefit from filling these gaps in knowledge.

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